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1160 W. Orange Grove Ave., Arcadia, California 91006, U.S.A.

COURTSHIP AND MATING BEHAVIOR OF THE FIERY SKIPPER, *HYLEPHILA PHYLAEUS* (HESPERIIDAE)

IRENE SHAPIRO

Graduate Group in Ecology,
University of California,
Davis, California 95616[1]

ABSTRACT

The courtship and mating behavior of *Hylephila phylaeus* (Hesperiidae) was studied by introducing dead and live tethered wild and laboratory reared females to wild males in the field. The hypothesis that wing movement elicits the male's initial investigative response in this species was tested. Entire courtship sequences resulting in successful matings were obtained with 18 live virgin females, indicating that males are less responsive to previously mated females.

INTRODUCTION

The problem of locating and successfully mating with a conspecific is of primary importance in the perpetuation of a species. Not only must potential mates recognize one another as opposed to closely related secies, but a synchronization of reproductive cycles must occur so as to bring members of the opposite sex together at the proper time of year. Only by studying the courtship and mating systems of individual species can theories pertaining to the significance of various aspects of such systems be validated.

The present study deals wi h the courtship and mating system of a Lepidopteran, the fiery skipper, *Hylephila phylaeus* (Hesperiidae). This species is abundant in the Sacramento Valley of California, where it is multiply brooded, having up to five generations per year. The larval host is Bermuda grass, *Cynodon dactylon* (Gramineae). *H. phylaeus* can be classified as a perching species as defined by Scott (1974c), i.e. males perch on projecting objects such as leaves, pieces of paper, and tall blades of

[1]Present address: 1005 S. Park Victoria Dr., Milpitas, California 95035.

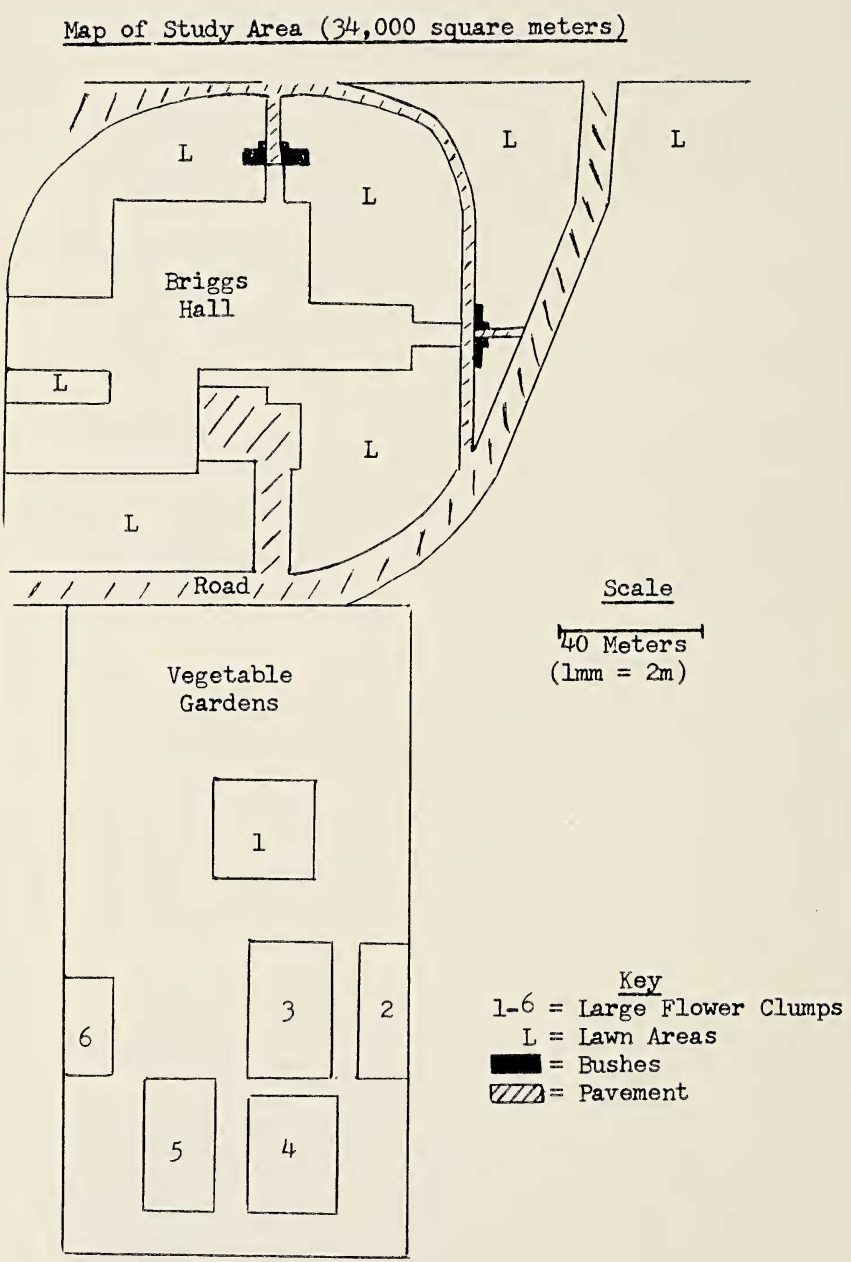

Fig. 1.—Map of Study Area (34,000 square meters)

grass on lawns and vacant lots in residential areas. Perching males fly towards and "investigate" moving objects such as other butterflies of the same or different species, other insects, and bits of leaves blown by the wind. The hypothesis that movement (specifically wing fluttering movement) elicits the male investigative response in this species was tested in the field.

MATERIALS AND METHODS

The study was conducted on the University of California, Davis campus throughout the periods of September to November, 1973 and June to December, 1974. The 34,000 square meter study area consisted of a 12,300 square meter lawn area of *Cynodon dactylon, Poa pratensis, Agrostis alba,* and *Festuca rubra,* which was separated by a road (10 meters in diameter) from a 21,700 square meter flower and vegetable garden that served as a food source for adult *phylaeus* (see Map Fig. 1). Male perching and investigative behavior were observed on the lawn area, while courtship and mating behavior experiments were conducted in the vegetable gardens because of the greater density of *H. phylaeus* there.

In order to determine the behavioral components involved in a complete courtship sequence, dead and live wild male and female *H. phylaeus* were presented to wild males in the field. A modification of the technique devised by Tinbergen et al. (1942) was used: butterflies were cooled for about ten minutes at 12°C so as to facilitate handling, and a quick-drying epoxy cement was applied to the dorsal surface of the thorax while a fine piece of fishing line was held in position until the glue dried (about three minutes). The fishing line was then attached to a rod which could be dangled in front, above or to the side of males at a distance of up to 1.8 meters from the observer. When fishing line was properly mounted, no difference from normal rapid flight movement was observed, except that individuals could not fly farther than a 1.8 meter diameter circle around the observer.

In a second group of experiments, laboratory reared females and males were presented in the same manner to wild males in the field in order to determine whether different results could be obtained with females known to be virgin. Results were recorded by notes and through use of a portable cassette tape recorder.

Table 1. 1973 Experiments with Tethered Wild Males and Females Presented to Wild Males in the Field (n = # males investigating or touching tethered skipper; N = total # males to which tethered skippers were presented; * = tethered skipper not flying, data discarded).

#	Tethered Females Presented to Wild Males						Tethered Males Presented to Wild Males						Tethered *Eufala* Presented to Wild Males					
	Male Investigated			Male Touched			Male Investigated			Male Touched			Male Investigated			Male Touched		
	n	N	%	n	N	%	n	N	%	n	N	%	n	N	%	n	N	%
1	10	12	83	2	12	16.7	9	10	90	2	10	20	10	10	100	1	10	10
2	10	11	91	4	11	36.4	8	10	80	1	10	10	7	10	70	0	10	0
3	9	10	90	1	10	10	7	10	70	0	10	0	10	10	100	2	10	20
4	8	10	80	0	10	0	8	10	80	2	10	20	1*	10*	10*	0*	10*	0*
5	9	10	90	2	10	20	10	10	100	1	10	10	0*	10*	0*	0*	10*	0*
6	10	10	100	0	10	0	9	10	90	0	10	0	-	-	-	-	-	-
7*	3	10	30	0	10	0	-	-	-	-	-	-	-	-	-	-	-	-
8*	0	10	0	0	10	0	-	-	-	-	-	-	-	-	-	-	-	-
Total	56	63	89	9	63	14.3	51	60	85	6	60	10	27	30	90	3	30	10

(No significant difference at .05 level between female, male, and *eufala* tethered skippers, using the t-test of difference between two means).

RESULTS

1973 Experiments with Wild Females and Males Presented to Wild Males

All experiments with dead male and female *phylaeus* failed to elicit courship behavior from wild males in the field. 13 dead females and 15 dead males presented to 10 wild males apiece elicited no responses, even when tethered skippers were dangled from fishing line directly in front of males. 2 dead females elicited an approach response, investigative behavior, from one of ten males apiece. In both instances, males immediately departed without touching or following the females. As a control, all tethered animals were also presented to 10 wild females apiece, and negative results were obtained in all cases.

Experiments with live *phylaeus* yielded more positive results on the preliminary phases of courtship. Data from 8 female and 6 male *H. phylaeus* were obtained. Both males and females elicited investigative behavior from wild males. When a tethered skipper was moved past a male at a distance of 0.3 to 0.6 meters, the male usually flew toward and often touched it with his head and antennae. A few males followed the tethered skipper for several feet, but most immediately departed, returning to an area near their original position. All tethered animals were presented to 10 wild females apiece, and no responses were elicited.

Five Eufala skippers, *Lerodea eufala,* were used in another group of experiments. In this species, the sexes are phenotypically alike, both being an overall brown-gray color with a peppering of small white spots on the upperside of the forewing. Investigative behavior and touching behavior were again elicited when live tethered *eufala* were presented to wild male *phylaeus,* and no responses were elicited when presented to wild females.

Results suggest that the fluttering of the wings during flight is a stimulus necessary to induce investigative behavior in males, since in all but two instances where a tethered skipper did not flutter its wings but merely hung at the end of the line, males did not respond. Differences in responses to female and male *phylaeus* and *eufala* were not significant at the 95% level using the t-test of difference between two means. This further substantiates the hypothesis that the fluttering of the wings may be more important than color or scent in initiating the first stages of courtship in *H. phylaeus* (Table 1).

1974 Experiments with Virgin Females and Males Presented to Wild Males

Results obtained in the 1974 experiments support the hypothesis that the fluttering of the wings is an essential stimulus to elicit investigative behavior in males. 16 females did not fly when presented to 10 males apiece, and subsequently failed to elicit a response in all 10 males. One female that failed to flutter its wings did elicit investigative behavior in three of 10 males, while two more non-flying females stimulated approaches in one of 10 males apiece. It was also found that feeding males usually failed to respond to tethered skippers. Out of a total of 71 trials with 16 female *phylaeus*, only 3 feeding males were stimulated to investigate; the other 68 males continued to feed.

Because no complete courtship sequences could be induced in the 1973 experiments with wild females, it was hypothesized that perhaps only virgin females could provide the correct stimuli necessary to elicit a sequence resulting in a successful mating. Therefore, in 1974, laboratory reared virgin females were used in the experiments. As a control experiment, 10 laboratory reared virgin males were also presented to wild males in the field; results were identical to those of 1973, where only the first phase of courtship, investigative behavior, was elicited. Experiments with virgin females, however, produced 18 successful matings. A description of the various phases in the courtship sequence of *H. phylaeus* is as follows:

Phase 1 — Investigative Behavior: the male flies toward and may touch a passing female.

Phase 2 — Settling Behavior: the male lands behind the female as she settles on a leaf, flower, or the ground.

Phase 3 — Head-Wing Behavior: the male, while situated at the rear of the female, thrusts his head between the female's hindwings, touching the upper surface of her wings and the rear of her abdomen with his head and antennae; males often thrust themselves so far forward that they are able to touch the upperside of the female's forewings.

Phase 4 — Fluttering Behavior: the male rapidly flutters his wings while moving laterally to the female and/or in front of her.

Phase 5 — Curving Behavior: the male, in a position posterior to the female, curves his abdomen in a U-shaped arc, so that his genitalia are in close proximity to the female's; the male genitalia are often extruded.

Phase 6 — Coupling Behavior: the male clasps the female with his harpes and apparently inserts his aedeagus into the female; after several seconds to several minutes, the male moves his body around so that he is facing in the opposite direction from the female (their bodies form a 180° angle).

Phase 7 — Uncoupling: copulation was terminated from 40 to 72 minutes after coupling except in one instance, when the mating pair separated after 27 minutes; it is not known whether a spermatophore was transferred or not, since the female flew away immediately after uncoupling. After separating, the male and female of all pairs observed either began feeding or flew away.

In the 18 successful courtships observed, overt female sexual behavior was minimal. The female usually remained stationary where she had settled, occasionally moving her antennae or walking forward several centimeters. In a few instances, females were observed to extrude genitalia, although this behavior also occurred during unsuccessful courtships. Shapiro (1970) proposed that such behavior in Pierid butterflies is part of a rejection display by unreceptive females. An identical display in Heliconiid butterflies, however, appears to have a pre-copulatory function, since in this group, the extrusion of the genitalia is related to pheromone release (Crane, 1957).

The duration of successful courtships prior to coupling ranged from ten seconds to three minutes and 30 seconds. Most were of short duration, and only five of 18 were longer than 40 seconds. Similar results were obtained by Brower et al. (1965), who found that the mean duration for 266 courtships in *Danaus gilippus berenice* was 40.4 seconds.

There was considerable variation in the sequence of phases as well as the repetition of phases among individual courtships. Nine courtships were single-phased sequences, while the other nine had sequences with repetitious phases. All but three courtships began with investigative behavior followed by the settling phase (Table 2).

Only one successful wild courtship as opposed to 208 unsuccessful wild courtships was ever observed. The duration of the courtship was 15 seconds, and the duration of time in copula was 40 minutes. The courtship was single-phased and was sequentially analogous to successful courtships in the experiments with laboratory reared virgin females.

Seven cases of carrying pair behavior were observed. In all cases, the female flew while carrying the quiescent male. Such behavior occurred only when the pair was disturbed in some way, such as by other males attempting to court the female or when touched by the investigator.

Table 2. 1974 Experiments with Virgin Females Presented to Wild Males in the Field - Sequence of Phases in Successful Courtships.

Female #	Sequence of Phases	
1	1-2-4-5-6-M	
2	1-2-3-4-5-6-M	
3	1-2-5-6-M	
4	1-2-5-4-6-M	Courtship Sequences
5	1-2-5-6-4-M	with Single Phases
6	1-2-5-4-6-M	
7	3-4-5-6-M	
8	1-2-3-4-5-6-M	
9	1-2-3-5-6-M	
10	1-2-5-4-6-P-5-6-P-6-M	
11	1-2-5-4-3-5-6-M	
12	1-2-4-3-5-6-P-5-6-4-Fl-2-5-6-M	
13	2-5-3-4-6-4-P-5-4-6-S-P-3-4-5-4-6-M	Courtship Sequences with
14	1-2-5-6-P-5-6-M	Repetitious Phases
15	1-2-4-5-6-P-5-6-P-5-6-4-M	
16	1-2-5-6-4-P-6-3-4-M	
17	1-2-5-3-4-S-6-P-5-3-4-S-5-3-4-S-6-5-3-4-6-M	
18	2-4-3-4-5-6-FD-2-6-P-5-6-P-4-6-M	

Key

1 = Investigative Behavior
2 = Settling Behavior
3 = Head-Wing Behavior
4 = Fluttering Behavior
5 = Curving Behavior
6 = Coupling Behavior
M = Successful Mating
P = Female Pulled Away
S = Female Shuddered
Fl = Courtship Disrupted by Another Male
FD = Female Deserted

Unsuccessful Courtships with Virgin Females

The courtship sequence can be terminated by either the male or the female after any of the first six phases in any of several ways. The most common cause of unsuccessful courtship was disruption by other males, which resulted in the courting male leaving the female and flying after the other male. Such investigative behavior often resulted in "chases" between two or more males to areas far removed from the origin of the encounter. 41 out of 88 unsuccessful courtships ended in this type of disruption behavior.

36 out of 88 courtships ended in male desertion behavior, where the male departed to a nearby flower or leaf. Such behavior may be elicited by a female rejection display called shuddering behavior, in which the female rapidly flutters the forewings and hindwings, which are opened at about a 45° angle from one another. Shuddering could be elicited either by head-wing behavior, fluttering behavior, or curving behavior and was often accompanied by movement a short distance away from the male. 28 of 36 courtships terminating by male desertion occurred after the female had shuddered once or several times.

These observations are in sharp contrast to the successful matings observed, where there were 16 out of 18 courtships in which the female did not shudder. It may be significant to note that the two females that did not shudder had repetitious courtship sequences, and that neither shuddered during the final sequence culminating in a successful mating.

Another female display which may be a rejection is the raising of the abdomen up and away from the male's genitalia during coupling. In all cases such pulling away behavior resulted in an uncoupling of the pair.

Courtships were also terminated by female desertion, where the female flew away from the male to another area. Only 11 out of 88 courtships ended in this manned (Table 3).

Unsuccessful courtships with virgin females were longer than unsuccessful courtships with mated females. Only the first phase of courship, investigative behavior, was elicited by mated females, while virgin females elicited at least one of the later stages of courtship (settling, head-wing, fluttering, curving).

Table 3. 1974 Experiments with Virgin Females Presented to Wild Males in the Field - Causes of Termination of Unsuccessful Courtships (in # of Observations).

Female Rejection Display	Disruption by Other Males	Male Desertion	Female Desertion	Total
Shuddering	17	28	7	52
Pulling Away	3	4	0	7
No Rejection Display	21	4	4	29
Total	41	36	11	88

DISCUSSION

Courtship and mating systems of insects have been shown to consist of progressive exchanges of stimuli between males and females; one partner's response to a stimulus elicited by the other releases the next response, and so on (Frings and Frings, 1958; Perdeck, 1957; Crane, 1957; Baerends, 1959). In *Hylephila phylaeus,* the initial investigative response of males appears to be elicited by movement, specifically the fluttering of the wings. Color of the wing does not appear to play a significant role, since males were equally attracted to both male and female *phylaeus,* despite the pronounced sexual dimorphism in this species, as well as to the darker *eufala* skippers. Size may possibly be a factor, although male *phylaeus* were occasionally seen to investigate larger butterfly species, such as *Vanessa cardui, V. carye, Colias eurytheme,* and *Pieris rapae.*

Magnus (1958) obtained similar results with *Argynnis paphia* (Nymphalidae). He proposed that the fluttering of the wings itself was not the decisive factor, but rather the rapid alteration of color versus absence of color when the wings are fluttered. He found that the intensity of the male response rose in direct proportion to the speed of color alteration. It is possible that a similar response may occur in *H. phylaeus,* since experiments thus far indicate that the fluttering motion of the wings is essential in eliciting a male response.

The investigative reaction appears to be related to the mate-locating system of various butterfly species: in perching species, the female must fly past the male to attract his attention; in patrolling species, it is the male that must fly past and locate non-flying females (Scott, 1974c). It would thus appear that color might be an important stimulus to the patrolling male, while the perching male would be more attracted to movement or quick flashes of color from fluttering wings. Thus far, the available data substantiates this hypothesis. In the perchers *Hypolimnas misippus* (Stride, 1957, 1958a and b), *Neominois ridingsii, Hesperia pahaska, Ochlodes snowi, Lycaena arota,* and *Amblyscirtes simius* (Scott, 1973a,b; 1974a), the first phase of courtship is elicited by movement of the female past the stationary male. In the patrollers *Argynnis paphia* (Magnus, 1958), *Erebia epipsodea* (Brussard and Ehrlich, 1970a,b), *Hypaurotis crysalus* (Scott, 1974b), and *Pieris rapae* (Obara, 1970), color of the female appears to be of primary importance in attracting males. In the patroller *Danaus gelippus berenice,*

Fig. 2.—Settling Behavior of *Hylephila phylaeus* During Courtship Sequence (Male Lands Behind Female).

however, Brower et al. (1965) stated that males are initially attracted to the female by seeing her in flight or while she is fluttering on herbage. Such behavior may be an artifact due to the procedure used by the investigators—females were released by hand into the air and all females that did not fly past the male were discarded from the results.

In *H. phylaeus,* the investigative reaction may also be related to carrying pair behavior. In order to carry the male during copulation, the female's wings must dry before mating occurs. Thus, the evolution of the wing fluttering movement as a stimulus to the male in courtship may also have evolved in response to the hardening of the female's wings signaling her readiness to mate.

Results of the field experiments on *H. phylaeus* suggest that in the next phases of the courtship sequence, where the male follows the female and settles near her, virgin females are considerably more attractive to males than are already mated females or other males. Firstly, there was no observable difference in length of the following reaction between tethered male or mated female *phylaeus;* secondly, all of the successful matings observed were with virgin females; thirdly, the unsuccessful courtships with virgin females were longer and more involved than those with mated females. Color would thus not appear to play a major role in eliciting the following response of males. It may instead be that a pheromone emitted by virgin females attracts males after the investigative approach. Scott (1973a,b; 1974a) found evidence that virgin females of *Neominois ridingsii, Hesperia pahaska, Ochlodes snowi,* and *Lycaena arota* may possess a pheromone that attracts males at close range (within about a meter). *H. pahaska* and *O. snowi* are fairly closely related to *H. phylaeus,* being in the same tribe.

In later stages of courtship in *H. phylaeus,* odor again may be the primary stimulus eliciting the male's responses, especially in head-wing behavior, in which the male's head is thrust between the female's hindwings, touching her genital region. Tactile stimuli may also be functioning. In these later stages, species-specific pheromones would be adaptive to insure against hybridization with other species.

The stigma or pouch on the forewing of males of various butterfly species has been proposed to carry a pheromone which stimulates the female during courtship (Scott, 1973b; MacNeill, 1964). In *H. phylaeus,* the fluttering behavior of the male may

Fig. 3.—Curving Behavior of *Hylephila phylaeus* During Courtship Sequence (Male Genitalia are Extruded).

serve to disperse the pheromone from the stigma. Males often moved laterally to and in front of the female while fluttering their wings, thus possibly surrounding the female with scent. Similar results have been observed by Scott (1973a,b; 1974a) in *Amblyscirtes simius, Hesperia pahaska, Ochlodes snowi,* and *Lycaena arota.*

The rejection display by females may function in minimizing energy expenditure. When a rejection display abruptly halts a male's advances, wasteful energy expenditure is reduced—the female's energy can then be directed towards oviposition. A rejection display is thus advantageous only if it stimulates the male to abruptly terminate a futile courtship, as was the case in *H. phylaeus.* As a consequence, wasteful energy expenditure on the part of the male is reduced. Also, in attempting to court a previously mated female, a male's chances of successfully contributing to the next generation are decreased (assuming that sperm precedence occurs, Tayor (1967)), simply because such a female is older and has a shorter survival time during which to oviposit than does a newly emerged virgin. However, if virgin females are in short supply, any male's fitness is likely to increase if he attempts to mate any female he encounters. This is likely to be the case in species like *H. phylaeus* in which the average female mates only once but males may mate multiply, so the frequency of unsuccessful courtships involving non-virgin females observed in the wild is not surprising.

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Fig. 4.—In Copula Pair of *Hylephila phylaeus*.

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